FAO Fisheries Technical Paper No. 116
(Distribution restricted)

FIRS/T116 (En)
Stock Assessment

LIBRARY
MAR 29 1973
FISH & WILDLIFE SERVICE

THE DYNAMICS OF THE MEAN-SIZE STATISTIC IN A CHANGING FISHERY

FOOD AND AGRICULTURE ORGANIZATION OF THE UNITED NATIONS
Rome, 1972

DOCUMENTS OF THE FISHERY RESOURCES DIVISION OF FAO DEPARTMENT OF FISHERIES

Documents which are not official FAO publications are issued in several series. They are given a restricted distribution and this fact should be indicated if they are cited. Most of them are prepared as working papers for meetings, or are summaries of information for use of Member Governments, organizations, and specialists concerned. These series are the following:

DOCUMENTS DE LA DIVISION DES RESSOURCES HALIEUTIQUES DU DÉPARTEMENT DES PÊCHES DE LA FAO

Des documents qui ne figurent pas parmi les publications officielles de la FAO sont publiés dans diverses séries. Ils font seulement l'objet d'une distribution restreinte, aussi convient-il de le préciser lorsque ces documents sont cités. Il s'agit le plus souvent de documents de travail préparés pour des réunions, ou de résumés d'information à l'intention des gouvernements des pays membres, ainsi que des organisations et spécialistes intéressés. Ces séries sont les suivantes:

DOCUMENTOS DE LA DIRECCION DE RECURSOS PESQUEROS DEL DEPARTAMENTO DE PESCA DE LA FAO

Esta Dirección publica varias series de documentos que no pueden considerarse como publicaciones oficiales de la FAO. Todos ellos tienen distribución limitada, circunstancia que debe indicarse en el caso de ser citados. La mayoría de los títulos que figuran en dichas series son documentos de trabajo preparados para reuniones o resúmenes de información destinados a los estados miembros, organizaciones y especialistas interesados. Estas series son las siguientes:

FAO Fisheries Report **FIR /R (No.)**
FAO Fisheries Circular **FIR /C (No.)**
FAO Fisheries Synopsis **FIR /S (No.)**

Special groups of synopses are identified by symbols followed by classification numbers based on indexed code of "ASFA":

SAST Data concerning certain species and fish stocks.

MAST Information on methods and subjects.

OT Oceanographic data.

IT Limnological data.

and

CART Information concerning fisheries and resources of certain countries and regions (FID/S).

Des catégories spéciales de synopses sont identifiées à l'aide de symboles suivis des chiffres de classification basés sur le code d'indexation de la « ASFA »:

SAST Données sur certaines espèces et populations de poissons.

MAST Renseignements sur des méthodes et des sujets.

OT Données océanographiques.

IT Données limnologiques.

et

CART Renseignements sur les pêcheries et les ressources de certains pays et régions (FID/S).

Grupos especiales de sinopsis se distinguen con las siglas siguientes, seguidas por números de clasificación que se basan en las claves de los índices de la « ASFA »:

SAST Datos relativos a ciertas especies y poblaciones.

MAST Sinopsis sobre métodos y materias.

OT Sinopsis sobre oceanografía.

IT Sinopsis sobre limnología.

y

CART Información sobre los recursos acuáticos vivos de algunos países y regiones (FID/S).

FAO Fisheries Technical Paper **FIRT/T (No.)**

Special groups of Technical Papers are identified by:

RE Indexed lists of experts and institutions drawn from Registers maintained by the Fishery Resources Division.

CB Lists of periodicals, special sections of "Aquatic Sciences and Fisheries Abstracts (ASFA)," special bibliographies and papers concerning documentation problems.

MFS Provisional editions of "FAO Manuals in Fisheries Science."

Des catégories spéciales de documents techniques sont identifiées à l'aide des symboles suivants:

RE Listes indexées d'experts et institutions tirées des registres tenus à jour par la Division des ressources halieutiques.

CB Listes de périodiques, des sections spéciales de la « Aquatic Sciences and Fisheries Abstracts (ASFA) », des bibliographies particulières et des articles sur les problèmes de documentation.

MFS Editions provisoires des « Manuels FAO de science halieutique ».

Grupos especiales de documentos técnicos se identifican por las siglas siguientes:

RE Listas índices de expertos y de instituciones tomadas de los registros que se llevan en la Dirección de Recursos Pesqueros.

CB Listas de periódicos, secciones especiales de la « Aquatic Sciences and Fisheries Abstracts (ASFA) », bibliografías especiales y trabajos relativos a los problemas de documentación.

MFS Ediciones provisionales de los « Manuales de la FAO de Ciencias Pesqueras ».

Some documents also have another identification, if, for example, they have been contributed to a meeting for which papers have been numbered according to another system.

Certains documents portent parfois d'autres numéros d'identification, par exemple s'ils ont été préparés pour une réunion dont les documents ont été marqués à l'aide d'un autre système.

Algunos documentos tienen también otra identificación si, por ejemplo, son contribuciones a una reunión cuyos documentos han sido marcados con arreglo a otros sistemas.

FAO Fisheries Technical Paper, No. 116
(Distribution restricted)

FIRS/T116 (En)
Stock assessment

THE DYNAMICS OF THE MEAN-SIZE STATISTIC IN A CHANGING FISHERY

by

F. Henderson
Fish Stock Evaluation Branch
Fishery Resources Division

FOOD AND AGRICULTURE ORGANIZATION OF THE UNITED NATIONS
Rome, October 1972

PREPARATION OF THIS PAPER

This paper gives some results of studies on the problems of stock assessment being carried out by the Fish Stock Evaluation Branch and other units of FAO, particularly in relation to the use of techniques other than the more conventional methods already described in existing FAO Manuals on Stock Assessment.

Distribution:

FAO Department of Fisheries
FAO Regional Fisheries Officers
Fishery Commissions
Selector SM

Bibliographic entry:

Henderson, F. (1972)
FAO Fish.Tech.Pap., (116):16 p.
The dynamics of the mean-size statistic in a changing fishery

E07. G. Population dynamics. Size of fish stock. Abundance - mean weight. Mortality. Recruitment. Growth rate. Selectivity. Mathematical review - equations, time series analysis.

CONTENTS

	Page
INTRODUCTION	1
THE EQUILIBRIUM STATE	2
DYNAMIC STATES	5
DISCUSSION	6
SUMMARY	10
Table I	11
Figures	12
REFERENCES	16

Digitized by the Internet Archive
in 2025

https://archive.org/details/fao-fisheries-and-aquaculture-technical-paper_1972_116

INTRODUCTION

The mean or average size of individuals of a stock has long been used as a simple criterion for assessing the status of a fishery. Generally decreasing size of individuals can be taken as an indication of either increasing mortality (usually equated with fishing mortality) or a decreasing growth rate (usually attributed to overcrowding). Independent information on the changes in growth rate may often be obtainable to separate the above alternatives. There are, however, other factors which may also affect mean size, the most important of which is the effect of changing recruitment.

Given some assumptions about the nature of the processes of mortality and growth, models such as those of Beverton and Holt (1957) may be used to derive estimates of total mortality from estimates of the mean size of individuals in the stock and estimates of growth parameters. For these relations to hold it is necessary to assume that the population is in equilibrium, that is, that there have been no recent changes in the parameters of the models. If this latter assumption is invalidated by recent or continuous change in the fishery, the mean-size statistic will be a function of the rate at which the latter changes are accomplished as well as the magnitude of the changes, that is, the history of the change becomes important.

Recency, in the above discussion, can be measured in terms of the lifetime of a cohort or the age of the oldest fish in the population. For many fisheries the equilibrium assumption is untenable. While substantial changes in fishing effort may quite obviously occur within the lifetime of a cohort, changes in environmental conditions effecting changes in natural mortality, growth and particularly recruitment may also occur rapidly or frequently. When these occur as trends, rather than "randomly", it becomes particularly difficult to assess the current status of the fishery. This paper was particularly motivated by the need for easily obtained indices of mortality in fisheries subjected to changing environmental conditions, such as in new reservoirs or bodies of water subjected to effects of human activities additional to the direct fishing activity.

In a system, such as a fish population, which exhibits delayed response to change, it is convenient to distinguish between the long-term or end response to a change in a particular factor which is then maintained at the new level (the equilibrium response), and the short-term response which depends on the way in which the change in the factor is accomplished (the transient response). In the situations examined here, the transient response can be expected to last no longer than the lifetime of the cohort (year-class) measured from the time the change is completed. Furthermore, if it can be assumed that mortality, growth and recruitment are independent parameters, then the equilibrium and the transient responses can be studied separately from each other and among the various parameters. The equilibrium responses are well-known, but are reviewed in the present context in the section on the equilibrium state. While the nature of the transient responses is also well-known, the problem of recognizing transients in a series of observations on a fishery has not been seriously attacked. In the succeeding sections, the possibility of recognizing these transients by considering the simultaneous changes over time in two kinds of observations is explored. The mean weight of individuals in the population and the abundance (catch/effort) can both be estimated from either fishing experiments or catch data from the fishery. As these two characteristics of a catch are affected differently by changes in mortality, growth, and recruitment, their joint behaviour over time (the trajectory of their behaviour) should provide more information on the source of changes than considering either alone.

THE EQUILIBRIUM STATE

If a fishery persists for some time in a steady state, the age or size structure of the population may be inferred by examining the history of a single cohort as it ages. That is, in a steady state population, the history of any set of recruits is independent of the year of hatching. While these conditions probably never occur in real fisheries, averages taken over an extended period of time may fulfil these conditions provided there are no significant trends in such factors as growth rate, mortality rates, recruitment and related conditions. Given an equilibrium, the mean age of the population ($\bar{t}$) is the inverse of the average instantaneous mortality rate (Z). Usually only a portion of the population is examined, say those of age greater than an age t_c, determined by the gear used in sampling. In this case

$$\bar{t} = \frac{1}{Z} + t_c \text{ (see Gulland, 1969)} \qquad (1)$$

While much of the subsequent discussion is applicable to data on the mean age of the population, it is generally easier to obtain data on size rather than age. The mean length in the sampled portion of the population may also be given in terms of the mortality coefficient by specifying an appropriate model relating length to age (see Gulland, 1969). For the purposes of the present discussion, and for many kinds of data where only total numbers and total weight in a sample (catch) are known, that is, where it is inconvenient to examine each fish separately, the mean weight of an individual may be easier to consider. Growth in weight in many fishes is nearly a linear function of age during the middle portions of the life history. Accepting some bias, it is assumed that

$w = G \cdot (t - t_c) + w_c$, where w_c is the weight of a fish of age t_c. The mean weight ($\bar{w}$) will correspond to the weight of individuals of age $\bar{t}$, hence

$\bar{w} = G(\bar{t} - t_c) + w_c$, where G is taken as the absolute rate of growth in weight with age. Substituting for the age expression in (1) gives

$$\bar{w} = \frac{G}{Z} + w_c \qquad (2)$$

Similarly, an expression for the number of individuals (N_c) age t_c or older is

$$N_t = N_c e^{-Z(t-t_c)} \qquad (3)$$

where N_c is the number of age t_c and e is a natural constant. This equation may also be given logarithmically, i.e.

$\log N_t = -Z(t - t_c) + \log N_c$, and is the equation of the conventional "catch curve" (Ricker, 1958).

The number of individuals surviving to age $\bar{t}$, is therefore, using (1)

$$N_{\bar{t}} = N_c e^{-Z(\bar{t}-t_c)} = N_c e^{-1}, \qquad (4)$$

which is also the number that survive to the weight $\bar{w}$, i.e. $N_{\bar{t}} = N_{\bar{w}} \approx N_c/2.7$.

It is also possible to infer, for equilibrium, the total abundance (P) of the population of individuals age t_c or older (weight w_c or heavier):

$$P = \sum N_t = N_c \left(1 + e^{-Z} + e^{-2Z} + \ldots\ldots\right)$$

$$= \frac{N_c}{(1+e^{-Z})} \quad \text{(Ricker, 1958)} \tag{5}$$

In the above, it is assumed that N_c individuals recruit to the population abruptly just prior to the observation of P. Where, as in many tropical species, recruitment occurs more or less continuously, or equivalently, where recruitment is abrupt but P is estimated by averaging observations spread throughout a year,

$$\bar{N}_c = \frac{N_c}{Z}(1-e^{-Z})$$

$$P = \frac{\bar{N}_c}{(1-e^{-Z})} = \frac{N_c}{Z}(1-e^{-Z}) \cdot \frac{1}{1-e^{-Z}} = \frac{N_c}{Z} \tag{6}$$

where $\bar{N}_c$ is the mean abundance of recruits over one year (Ricker, 1958).

Based on the above assumptions, which must necessarily yield only first approximations, at equilibrium we have

$$\bar{w} = \frac{G}{Z} + w_c, \text{ and} \tag{2}$$

$$P = \frac{N_c}{Z} \tag{6}$$

In order to provide a reference grid for the examination of changing conditions in the fishery, it seems useful to plot successive observations of $\bar{w}$ and P on a graph. Owing to the large variances generally associated with estimates of abundance (P), and the tendency for these variances to increase with increasing population size, I have plotted the logarithm of P rather than P. Normally, estimates of P will be relative estimates such as catch/effort, in which case N_c will be similarly estimated.

Before turning to non-equilibrium conditions, the changes in the point of equilibrium produced by a change in each of the above parameters may be plotted as in Fig. 1. These loci of equilibrium points may be obtained from the above relationships.

Change in total mortality. If the total mortality coefficient changes and then remains at the new level long enough for a new equilibrium to be established, the new equilibrium should fall on the equation obtained by eliminating Z from (2) and (6), i.e.

$$\bar{w} = \frac{G \cdot P}{N_c} + w_c, \text{ or using logarithms}$$

$$\bar{w} = \frac{G}{\bar{N}_c} \cdot e^{\log P} + w_c, \text{ or better}$$

$$\bar{w} = G\, e^{\log(P-N_c)} + w_c$$

This line is plotted on Fig. 1, with an arrow indicating the direction corresponding to an increase in total mortality Z. Note that a change in Z will change the equilibrium values of both $\bar{w}$ and P.

Change in growth rate. In equations (2) and (6), it is apparent that a change in the equilibrium point brought about by a change in G will effect a change in $\bar{w}$, but not in P. The locus of change is shown in Fig. 1 along with an arrow indicating the direction corresponding to an increase in G.

Change in recruitment. A change in the recruitment, N_c, will affect the total population P but not the mean weight $\bar{w}$. Again the locus is shown with an arrow corresponding to an increase in N_c.

Change in the weight at recruitment (change in selectivity). In the preceding discussions recruitment has been equated with the age or size at which fish enter the population summed in P. For simplicity in the models, it has also been assumed that all the history (mortality, growth, recruitment) of the part of the population younger than t_c (smaller than w_c) is summed up in the parameters N_c and w_c. Therefore the values N_c and w_c are determined by the methods used to obtain estimates of P and $\bar{w}$, i.e. correspond to the selectivity of the gear used. The models also assume that all fish age t_c and older are equally represented in obtaining the estimates of P and $\bar{w}$, an assumption that will almost never be accurate, but under many circumstances may be tolerable.

Continuing to equate N_c with a recruitment, but now assuming that this remains constant while new gear is used that only catches individuals weighing w_c' or more:

$$N_c' = N_c \, e^{-Z(w_c'-w_c)/G}$$

But now

$P = \frac{N_c'}{Z}$, and $\bar{w} = \frac{G}{Z} + w_c'$, since they are estimated for the new gear. Hence, substituting and converting to the logarithmic form (base e)

$$\bar{w} = -\frac{G}{Z} \log P + \frac{G}{Z} \left(1+\log N_c/Z\right) + w_c$$

This is linear with respect to log P and $\bar{w}$ with slope $-\frac{Z}{G}$, and gives the locus of equilibria for varying selectivity, i.e. varying w_c'. It is plotted in Fig. 1 with an arrow indicating the direction of change produced by an increase in the minimum size taken by the gear. Note that the intercept of the log P axis is

$$1 - \frac{Z}{G} w_c - \log \left(\frac{N_c}{Z}\right)$$

The intercept is, therefore, a function of the size at which recruitment (N_c) is considered to occur.

It is interesting to note that this is a transformation of the catch curve, referred to earlier, for a population in equilibrium in which the logarithm of the abundance of a given size (age) class is replaced by the logarithm of the abundance summed over all classes of size w_c and larger. In the special situation where there is evidence of equilibrium and a multimesh fleet of gill nets is used as a sampling tool, these sums could be readily obtained for the remaining mesh sizes after the smallest are dropped one by one from the data. Plotting logarithms of the adjusted sums against w_c, which should be known for each mesh size, is equivalent to plotting the more conventional catch curve.

While each of the above changes produces a characteristic change in the equilibrium point, it should be noted that a new equilibrium may be obtained by several combinations of changes in the parameters modelled. Clearly, observations of equilibrium values of P and $\bar{w}$ are insufficient to uniquely determine values of any of the parameters. At least two of the four parameters Z, G, N_c, and w_c must be independently estimated in the steady state (equilibrium) population in order to estimate the remaining two from the given data, i.e. mean weight and population abundance.

During the transition between equilibria, the above equations (2) and (6) are not valid, as each of the age groups or weight groups comprising P will have had different histories. The next step is to distinguish between the (a) locus of points representing successive observations of P and $\bar{w}$ (generally annual intervals) during a period of transition and (b) the loci, described above, of equilibrium values of P and $\bar{w}$. The former locus (a) may be called the "trajectory" of the population describing transitional behaviour.

DYNAMIC STATES

In the derivation of Fig. 1, it was assumed that mortality rates, growth rates, recruitment and selectivity were all independent of each other and of age or size; and further, that they remained constant long enough to permit the population to attain a constant size structure. It is now proposed to relax the latter assumption, making these parameters functions of time, and looking at the most likely, albeit simplified, kinds of changes that would occur in practical fishery problems. For this, I have used a pencil-and-paper simulation, assuming as a base a population with recruitment N_c = 1,000, annual mortality rate = 0.5 (Z = 0.7), growth rate = 1 unit/year, weight at first capture = zero and considered initially in equilibrium. For this discrete model, equations (2) and (6) become, respectively:

$\bar{w} = \frac{G}{m}$ and $P = \frac{N_c}{m}$, where $m = 1 - e^{-Z}$, that is m is the annual mortality rate as distinguished from the instantaneous mortality rate.

Change in recruitment. The most troublesome parameter to model in studies of fish populations is that of recruitment, owing to the apparent wide fluctuations in recruitment for many species from year to year. Table I shows the simulation adopted corresponding to an abrupt increase in N_c from 1,000 individuals to 2,000, with the resulting values of P and $\bar{w}$ plotted in Fig. 2, line A. Note that, in the simulation, the new rate of recruitment is maintained until the population is again in equilibrium. I have also shown in Fig. 2 the results of reducing the recruitment to 500, line B, and of an increase to 2,000 which occurs in one year only, returning to 1,000 until equilibrium is reached, line C.

For an increase in recruitment, the first response is an increase in P equal to the extra recruits and a decrease in the mean weight corresponding to the small size of the added individuals. If the increased recruitment is continued, the trajectory approaches the new equilibrium point with the mean weight returning to its initial value. During the period of transition, the mean weight and population size clearly do not lie along the corresponding locus of changes in the equilibrium values. Hence the equilibrium loci corresponding to a change in recruitment on the one side and a change in "selectivity" on the other. If there is a steady increase in recruitment, line D, there results a gradual reduction in the effect of change on the mean weight even though the overall population continues to increase.

It is thus apparent that real changes in recruitment to the population displace the mean weight from its equilibrium value (i.e. for given Z and G) and that the direction of the displacement depends on the direction of change in the recruitment. Therefore, if the mean weight statistic is used as an index of mortality, as in equation (2), the mortality will be overestimated if the population has recently been subjected to increased recruitment and underestimated if the recruitment has recently diminished.

Change in total mortality. The population trajectory produced by a change in the mortality rate shows quite a different behaviour. In this case a change to a new level of mortality produces an immediate change which is not far from the direction of the change in the equilibrium point that would be established if the new level is maintained. The full effect of the change, however, remains delayed. The results of simulation are shown in Fig. 2 (E) with annual rate changed to 0.75 ($Z = 1.4$). The same base population was used as for the recruitment analysis, assuming that the mortality rate shifted simultaneously within a year for all fish of size w_c and larger and remained at the new level until a new equilibrium is reached. Generally, changes in mortality can be associated with fishing mortalities in practical problems, large "random" fluctuations in mortality being relatively much rarer than in the case of recruitment. The effect is to make it easier, in general, to identify trends in mortality than in recruitment.

Comparing initial changes with the final equilibria, it is interesting to note that in the region of low mortalities the initial changes are small and the new equilibria are reached only after a considerable period of time, whereas the opposite behaviour occurs in the region of high mortalities. While this is entirely to be expected, it emphasizes that a heavily exploited fishery should be expected to respond more rapidly to change than one that is lightly exploited.

Change in growth rate. Within the limits of the assumptions stated earlier, specifically that the parameters are independent, a change in growth rate will effect a change in the mean weight of the population but not a change in population number. The trajectory of change will therefore lie along the locus of equilibrium changes (Fig. 1). Again it will take some time for the shift to be completed, as initially the larger fish will undergo a smaller relative change in size than the small fish. Eventually, if the new growth rate persists, all fish will be subjected to the same growth history and a new equilibrium is reached.

Change in weight of recruits or selectivity. If the sampling or fishing gear is changed to a new selectivity, the structure of the population remains unchanged according to the model, hence the change will be prompt. The assumptions of the model are substantially violated, however, if the change in gear is accompanied by a change in the total mortality rate. The change depicted in Fig. 1 is appropriate for data obtained from small-scale "exploratory" fishing, while in data taken from commercial operations both the change in selectivity and the change in mortality must be considered. The latter will be of particular significance if the mortality rate is markedly age specific.

DISCUSSION

The generalized sorts of models exemplified in the preceding discussion fall far short of describing the complexities of the behaviour of fish populations. Nevertheless, by focusing attention on specific contributory factors, it is sometimes possible to see elements of the behaviour of these populations in a different way, and this is what I have attempted to do. It remains essential, however, to keep in mind the details deliberately overlooked, and to approach specific problems with some idea of the probability that any particular assumption is violated in the instance at hand.

Variation in Recruitment

The particular choice of variables taken in this paper was based on the conviction that the most likely source of year-to-year variability in the apparent mean size of the population is variability in the annual recruitment. That is, given a difference between two successive annual estimates of the mean size of individuals, large enough to suggest real rather than sampling differences, the most likely immediate "cause" of this difference is a change in the number of individuals recruited to the population between the two years. A change in recruitment, in this case, might have resulted from a number of other changes such as the number of eggs spawned, pre-recruitment mortality, or the spatial distribution of the young fish relative to the older fish. It can be further argued, that in many populations the number of eggs spawned is relatively less important by a large margin than early mortality in determining the current level of recruitment. If so, then the assumption that the recruitment (N_c) can be treated independently of the population abundance is likely to be reasonable at least in short series of data. In this regard, Cushing's (1971) recent remarks should be noted in which he points out that constancy of recruitment should be regarded as evidence of density dependent regulation rather than of environmentally limited recruitment.

It is apparent from the simulation given that secular trends in recruitment, where recruitment continues to increase (or decrease) over a number of years, can only result in a continued trend in mean weight if the recruitment grows at a higher rate than the population. A special case occurs when there is continued failure of recruitment and the mean weight continues to increase until the last fish die, or when recruitment increases so rapidly that all fish larger than the recruits remain a negligible portion of the population. In the usual case, longer term trends in mean size are not likely to be attributable to changes in recruitment.

The foregoing argument points up a special difficulty in the assumptions which have arisen by equating recruitment with age at first capture. In order to treat mortality and recruitment as independent parameters, it is required that pre-recruitment and post-recruitment mortality be independent, with a dividing line at w_c (or t_c). This condition is partly fulfilled in fisheries under exploitation where fishing mortality acts above w_c and not below. One may also argue that the immediate causal factors of death in very young fish are quite different from those of adult fish owing to changes in predators, food habits, and habitat preference. Nevertheless some dependence between the apparent recruitment of small fish and apparent mortality of larger fish should be expected, and if it exists will be enhanced both by lack of sharpness of the selectivity curve and by a strong tendency for the estimated average weight of individuals to be weighted in favour of newly recruited fish.

Variation in Mortality

The models above have not separated fishing and natural mortalities. In most practical situations one assumes that a change in total mortality over time is associated with a change in fishing mortality. The assumption arises from the association of natural mortality with an environment that is not changing significantly over time. In following changes in new reservoirs or changes related to environmental modification by human activities unrelated to fishing, the assumption is clearly less valid. In this regard, it should also be pointed out that the simpler criteria for evaluating the exploitation rate (F/Z) in relation to the capability of a particular stock to support exploitation (Gulland, 1970) assume that the estimate of the natural mortality rate is an estimate of the natural rate that would be exhibited if the stock were in equilibrium and unexploited (virgin). For such reasons, in situations where it is strongly suspected that non-fishing mortalities are changing, criteria based on total observed mortality, and an independent estimate of the "typical" natural mortality of the species concerned (see Beverton and Holt, 1959; Gulland, 1969) may be much less misleading than criteria based on direct observations. In cases where quite

independent estimates of the two forms of mortality are available, rather more detailed analyses of the condition of the stock than those outlined here will be available for use.

Another feature of the dynamic simulations obtained here is that the duration of a "transient" response is not so much dependent on intrinsic "natural" mortality of the species, but rather depends on the actual replacement rate of the present stock, i.e. on the total mortality rate. Transients occurring in the lower half of the graph in Fig. 2 are completed more quickly than those in the upper half, as noted earlier. This also implies that a heavily fished stock is more likely to be found in a condition near "equilibrium" than a lightly fished stock.

Variation in Growth Rate

While the transient behaviour produced by a change in growth rate is distinct in its effects on mean weight from the other types of transients, in practice a change in growth rate will rarely be independent of changes in the other parameters to any satisfactory degree. Year-to-year variability in growth, however, may typically be of much lesser magnitude than recruitment. Unless there is a well founded reason for assuming that the growth rate is not changing over time, mean size statistics can only be interpreted in terms of mortality and recruitment if independent estimates of growth rate can be obtained. In the reservoirs of tropical Africa, growth information is difficult to obtain. Indeed the difficulty of aging individuals is the main reason for using an integral property like mean weight, rather than age specific parameters or catch curve analysis, in following the changes in the fishery. Fortunately, information about growth in the weight range just larger than w_c is more important than in the upper ranges of weight in interpreting the dynamic events, and this information can sometimes be obtained from length and/or weight frequency diagrams.

Variation in Selectivity

Both the initial models and the dynamic simulation given here assume that the gear used in sampling or fishing will take no fish less than w_c in weight. Departure from uniformity in the latter fraction will make the apparent mortality rate of the sample different from the mortality rate of the population, that is will introduce a bias in the estimates. It will also make the apparent weight vs. age function different from that of the population with attendent bias. If the gear exhibits a narrow range of selection, the biases obviously become serious. If the selectivity curve is reasonably broad and flat, the biases become similar to those introduced by the assumption of a constant absolute growth rate and a constant mortality rate over all size range above w_c. If gill nets are to be used as the sampling tool, it is clear that multimesh fleets will be necessary to achieve reasonably "flat" selectivity.

If one considers only changes in the size of first capture, leaving the rest of the selectivity curve unchanged, a change in w_c will produce an immediate shift, without any transients, to the new equilibrium corresponding to the change in w_c. However, if the change is made in the fishing gear, rather than sampling gear, the population mortality rate will be affected for the size classes included between the old and the new w_c. This change will produce a transient of the sort produced by a change in recruitment (graph A, B in Fig. 2). Clearly the transient response becomes quite complex if only a few of the parameters vary over time and there are thus great advantages in keeping the selectivity as constant as possible through the period of study. The transient behaviour of the mean weight characteristic will be more easily studied by properly designed direct sampling programmes than from most commercial catch data.

Analysis of the changes in mean weight as a time series

The more usual procedure for studying the changes in a particular variable over time is to look at the behaviour of the variable as a time series (e.g. Fig. 3). For any particular observation in time one is anxious to know to what extent the value of the variable is dependent on current conditions (Z, G, N_c, w_c), to what extent it is dependent on past conditions, and to what extent it is dependent on sampling errors. If the sampling has been done carefully, the sampling error associated with a particular observation will not be dependent on the error of the previous measurement. In other words, the error portions of the observation should not exhibit any meaningful history. As the effects of a change in the fishery conditions cannot take full immediate effect, such changes will establish a trend that insures that an observation will to some extent be correlated with a previous measurement. In the region of time during which a change in the conditions is occurring and for some time afterwards, the series of observations of mean weight will be autocorrelated. During any period in which the variance associated with sampling error (estimated by replicate "simultaneous" observations) is large compared to the covariance of successive observations, one cannot be convinced of a change in the fishery conditions during that period.

If the conditions in the fishery vary randomly, autocorrelation will be introduced among successive observations even though there is no overall trend, i.e. the "average" conditions have not changed. A persistent change, a true trend, will extend the region of autocorrelation over a period of time in excess of the lifetime of a transient, equivalent in our case to the time that it takes for a particular set of "recruits" to disappear from the fishery. This latter time is a function of the total mortality rate. Theoretically, therefore, a covariance-autocovariance spectrum of replicate time series should enable one to distinguish between sampling error (no autocovariance), transients (autocovariance in among closely spaced observations and trends autocovariance among distantly placed observations).

The advantage of examining population abundance as well as mean weight is that the autocovariance spectra of population abundance and of the mean weight of individuals in a catch may be expected, a priori, to differ with respect to trends, even though both will exhibit transients. Plotting the two variables against each other produces, in a general sense, a pattern that allows subjective separation of these autocovariance spectra. Often, indeed, the observer has additional information at hand such as the relative magnitudes of random vs systematic changes in fishing effort, the time at which change is expected, and so on.

A practical illustration

In Fig. 4 are plotted successive annual values of mean weight of individuals and catch/effort for a trout population in Colombia. The data are derived from an annual fishing contest, the Concursos Internos, for the years 1953 to 1970. In Fig. 3 the mean weight has been plotted as a function of time and a definite trend is apparent. The obvious question of interest in management is the question of extrapolating the apparent trend. The fitted solid line suggests greater peril to the fishery than would be evident if the dashed lines were fitted. The last few points are more pertinent than the others to such a question. In Fig. 4 there is some evidence of an "equilibrium" near 1.6 pounds, with no persistent change after 1963. The overall pattern for all years suggests strong yearclass fluctuations with a gradual improvement in recruitment (habitat improvement or perhaps stocking) and a nearly twofold increase in mortality rate (or decrease in growth rate!).

The trajectories of change in Fig. 4 seem to fit nicely into the sorts of patterns which might be expected from Figs. 1 and 2 (the diagonal line assumes an annual mortality rate of 1 and a growth rate of 1 pound per year in the range of interest - reasonable values for trout).

From the above it seems quite clear that the data prior to 1961 and 1962 are not pertinent to the extrapolation except as they provide estimates of the magnitude of year class fluctuations. While the points for the last three years (Fig. 4) are disconcerting with respect to the future of the fishery, they are not distinguishable from an increase in recruitment after an apparent drop in 1966 and 1967. The analysis therefore favours the dashed lines of Fig. 3. If the growth rate were known, the total mortality rate could be estimated for mean weight 1.6 pounds.

Fig. 6, however, is similarly drawn for a second contest involving the same population, the Concursos Nacionales. In this case catch/effort data were only available for the later years. This pattern, while suggesting a stable mean weight, fits expected patterns very poorly. Lacking any other evidence I can only conclude that the variability of the abundance estimates (no. caught/no. fisherman x hours of fishing) is considerably higher in this latter contest.

SUMMARY

Graphs of simultaneous observations of the mean-weight (or other average size criterion) and population abundance (e.g. catch/effort) may be useful in deciding which of several possible factors may be responsible for changes in the average weight of individuals in a population, even if environmental conditions in the fishery are known to be changing. Independent information on rates of growth, and control over the selectivity of the sampling method are also needed if reasonably secure inferences are to be made.

If the sample variance of the estimates is reasonably small relative to the observed changes over time, the pattern exhibited by successive observations may be compared with the patterns expected from simulation for various kinds of change in the population parameters. If there is evidence of a sudden and substantial change at a known point in time, the direction and magnitude of the first response is a useful predictor of the equilibrium response. Otherwise such a plot may primarily be useful in distinguishing real changes and trends in mortality from changes in size composition of the population brought about by variations in recruitment. The latter use requires much longer sequences of observations.

Table I

Calculation of the change in abundance and mean weight resulting from increase in recruitment

Age	Weight at Age	0	1	2	3	4	5	6	7	∞′
0	1	1 000	2 000	2 000	2 000	2 000	2 000	2 000	2 000	2 000
		1 000	2 000	2 000	2 000	2 000	2 000	2 000	2 000	2 000
I	2	500	500	1 000	1 000	1 000	1 000	1 000	1 000	1 000
		1 000	1 000	2 000	2 000	2 000	2 000	2 000	2 000	2 000
II	3	250	250	250	500	500	500	500	500	500
		750	750	750	1 500	1 500	1 500	1 500	1 500	1 500
III	4	125	125	125	125	250	250	250	250	250
		500	500	500	500	1 000	1 000	1 000	1 000	1 000
IV	5	62	62	62	62	62	125	125	125	125
		312	312	312	312	312	625	625	625	625
V	6	31	31	31	31	31	31	62	62	62
		188	188	188	188	188	188	372	372	372
VI	7	16	16	16	16	16	16	16	31	31
		109	109	109	109	109	109	109	219	219
VII	8	8	8	8	8	8	8	8	8	16
		64	64	64	64	64	64	64	64	122
VIII	9	4	4	4	4	4	4	4	4	4
		36	36	36	36	36	36	36	36	36
IX	10	2	2	2	2	2	2	2	2	2
		20	20	20	20	20	20	20	20	20
X	11	1	1	1	1	1	1	1	1	1
		11	11	11	11	11	11	11	11	11
Sum numbers		2 000	3 000	3 500	3 750	3 875	3 937	3 968	3 983	4 000
Sum weight		3 990	4 990	5 990	6 740	7 240	7 553	7 737	7 847	8 000
Mean weight		1.99	1.66	1.71	1.79	1.87	1.92	1.95	1.97	2.00
Log number		3.30	3.48	3.54	3.57	3.59	3.60	3.60	3.60	3.60

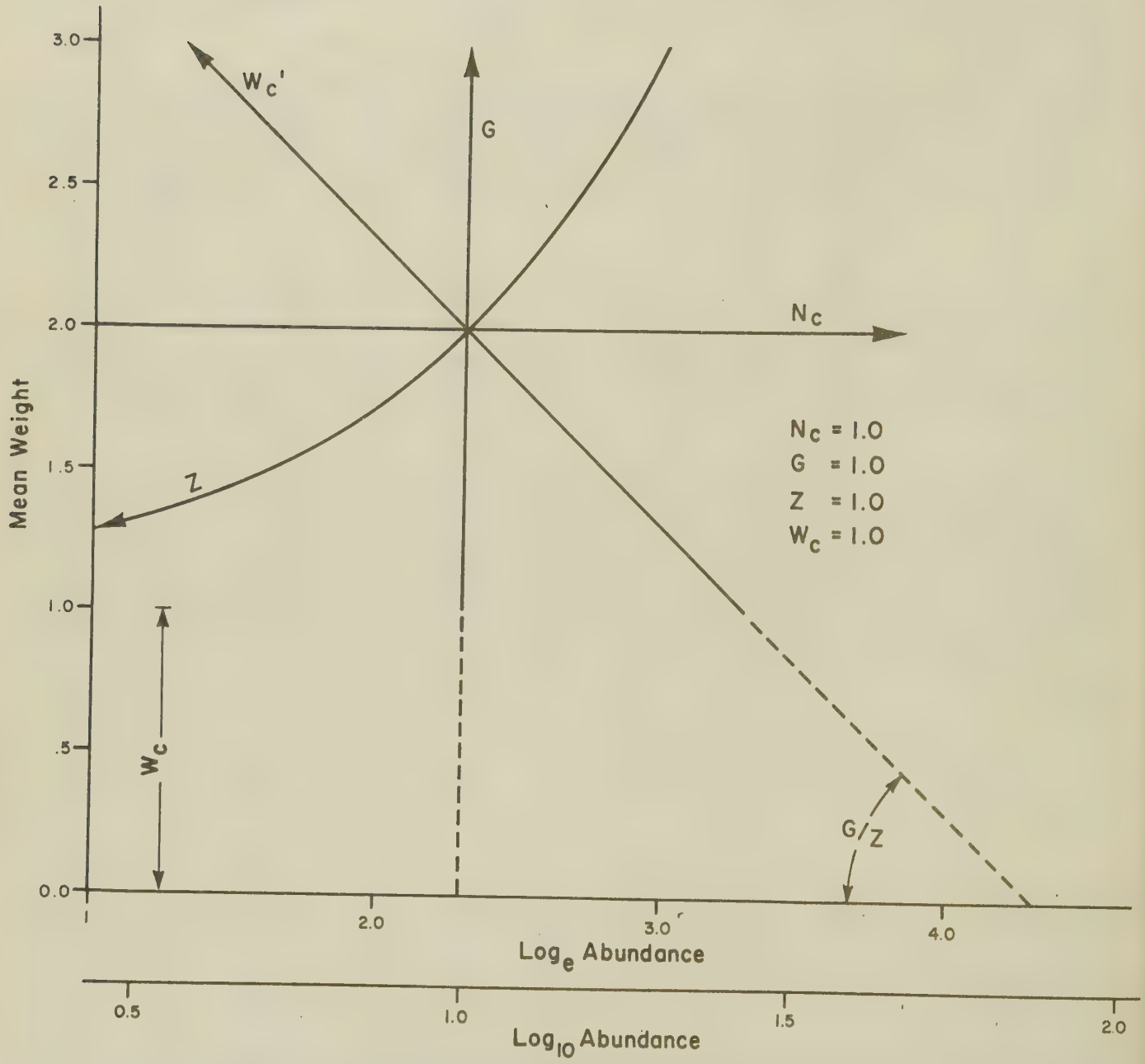

Figure 1 - Trajectories of Simulated Changes in Mean Weight and Logarithm Population Abundance

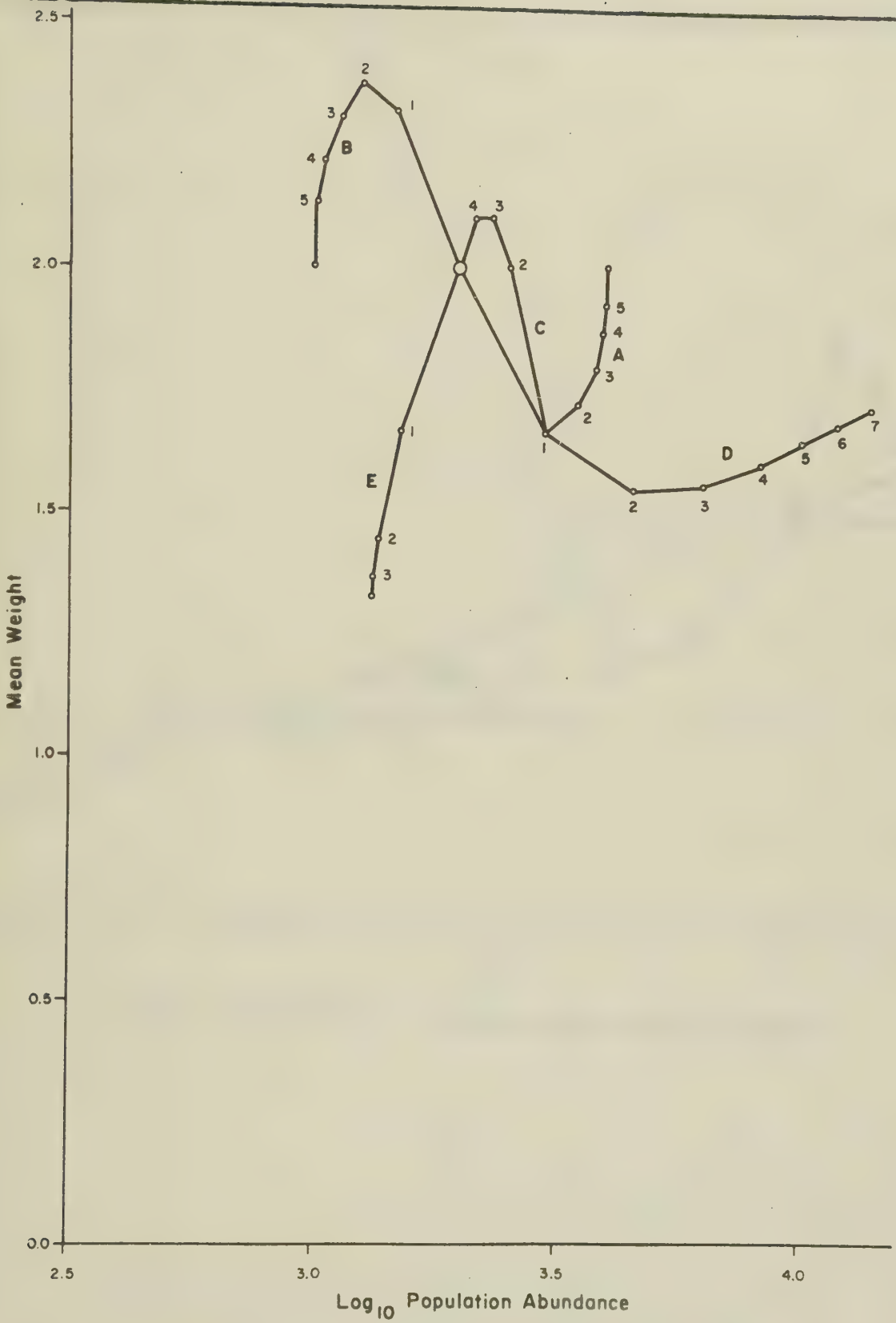

Figure 2 - Trajectories of Simulated Changes in Mean Weight and Population Abundance

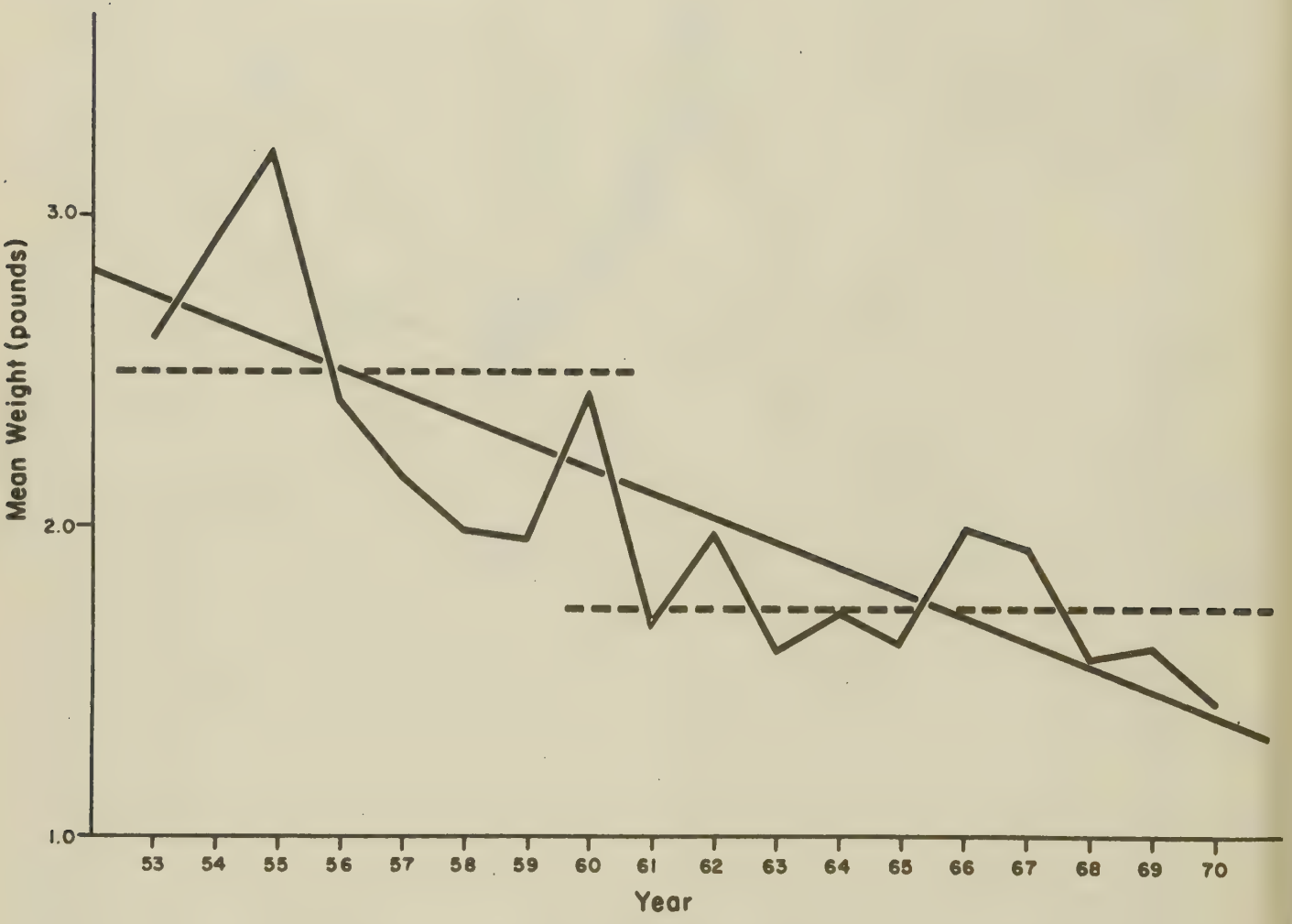

Figure 3 - Trends in Mean Weight - Colombian Trout Fishery

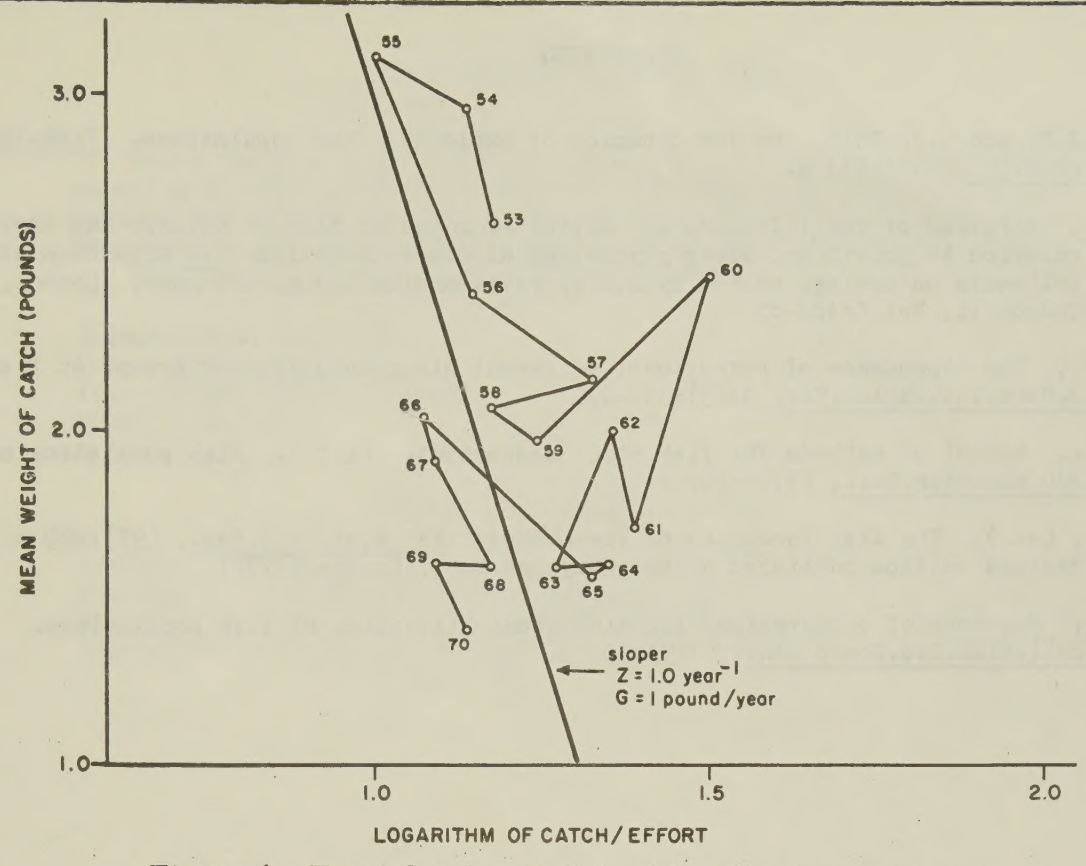

Figure 4 - Trout Catches in Colombia - Concursos internos

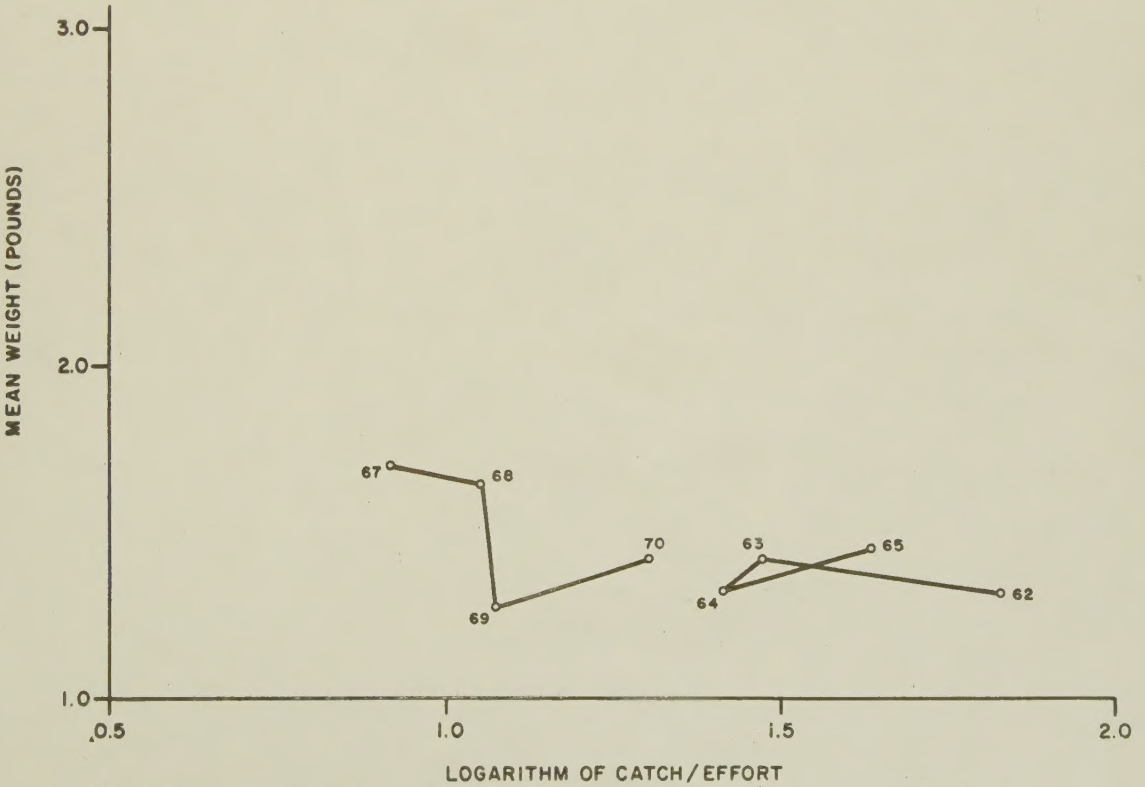

Figure 5 - Trout Catches in Colombia - Concursos Nacionales

REFERENCES

Beverton, R.J.H. and S.J. Holt, On the dynamics of exploited fish populations. Fish.Invest. Lond.(2), (19):533 p.
1957

_____, A review of the lifespans and mortality rates of fish in nature, and their relation to growth and other physiological characteristics. In Ciba Foundation colloquia on ageing, edited by G.E.W. Wolstenholme and M. O'Connor. London, Churchill, Vol.5:142-80
1959

Cushing, D.H., The dependence of recruitment on parent stock in different groups of fishes. J.Cons.Int.Explor.Mer, 33(3):340-62
1971

Gulland, J.A., Manual of methods for fish stock assessment. Part 1. Fish population analysis. FAO Man.Fish.Sci., (4):pag.var.
1970

_____, (ed.), The fish resources of the oceans. FAO Fish.Tech.Pap., (97):425 p. Revised edition published by Heighway and Sons, London (1972)
1970

Ricker, W.E., Handbook of computations for biological statistics of fish populations. Bull.Fish.Res.Board Can., (119):300 p.
1958

FAO FISHERIES TECHNICAL PAPER

This is one of a series of Technical Papers (see inside front cover) dealing with aspects of the work of the FAO Department of Fisheries, Fishery Resources Division, including the review of pertinent information on particular topics, to meet requests for assistance, for presentation to technical and scientific meetings, etc.

Extra copies can be obtained by application to:

Research Information Section
Fishery Resources Division
FAO, Via delle Terme di Caracalla
00100 Rome, Italy

(Papers issued since January 1971)

FIRD/T101	Computer programs for fish stock assessment	February 1971
FIRM/T102	Manual of methods for fisheries resource surveys	June 1971
FIR/T110	Fish and fisheries in the context of environmental concerns	December 1971
FIRS/T116	The dynamics of the mean-size statistic in a changing fishery	October 1972

WI/D3104/12.72/E/1/900